The basics of plant hydraulics

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MINI-REVIEW

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Abstract

This short text gives the fundamentals of plant hydraulics and its impact of their water relations and gas exchanges.

Thirst or starve!

Plant feed on atmospheric CO2. Photosynthesis is the chemical process by which plants transform atmospheric CO2 into sugar molecules in their leaves. The energy for this reaction come from the light, therefore leaves are flat. Plants 'eat' these molecules or assemble them into larger molecules to grow bigger. Photosynthesis also releases 02 in the atmosphere, but plants do not really care about this (we do!).

CO2 needs to enter into the leaves because photosynthesis takes place inside the leaves. Leaves are thus porous and cover of tiny holes (stomata) to let CO2 get in the leaf. As the CO2 concentration is low in the atmosphere (plants are delighted to know we increase it!), plants deploy many leaves to capture all the CO2 they need.

Leaves are nearly saturated with water, but the atmosphere is very dry, especially during day time. Even when air humidity is high (>80%), air is still much drier than turgid leaves.

When stomata are open to let few CO2 molecules move in, tons of H20 molecules escape through them. If stomata close to lower leaf water loss then less CO2 is capture and plant starve. Plants are really smart, but for some reasons they forgot to invent a membrane for their cells permeable to CO2 and impermeable to H20 molecules. There is no way around this problem, if they want CO2 to get in, H20 must get out. (Cactus found a smart solution, but I talk about cactus another time).

Plants have hence to face this cruel dilemma: die of thirst (stomata too open) or die of starvation (stomata too close). As plants really need CO2 they have chosen to waste a lot of water. This is why plants need so much water to grow and if you do not water them they grow less.

To compensate leaf water loss and maintain them hydrated and photosynthetically active, leave must be continuously irrigated with water. Land plant growth and survival are therefore highly dependent on the performance of a water transport system. This is where we finally talk about plant hydraulics…

Sap ascent in plants

Plants find the water they need in the soil to irrigate their leaves. That is what all these tiny roots are for: absorb water. Water is liquid in the soil, and water is also transported in this liquid state to the leaves. Water moves from the roots to the leaves in tiny pipes made of dead cells that form the xylem tissue. Continuous liquid water columns connect the leaves to the liquid water in the soil. These columns are 'attached' to the leaves thanks to high capillary forces that develop in the leaf cell walls. This is a very important point.

As I said, because leaves are in a very dry atmosphere, liquid water evaporates inside the leaves at the very top of the water columns. Water molecules then pass through stomata in a vapor phase to the atmosphere.

Water evaporation enhances the capillary forces, and these forces pull on the water columns putting them under tension. But, as water molecules are strongly attached together, water columns have a very high cohesion. When you pull on a rope, the whole rope moves up. The same is true for water columns: when evaporation pulls on them, the whole columns of sap ascent the plant and water is absorbed by roots at the other end. This was the tricky point, but Dixon & Joly figured out this "tension-cohesion" mechanism in 1895! The higher the evaporation in the leaves, the higher the tension in the water columns and the higher the absorption by roots. The mechanism is self-regulated and very cost-effective as all the energy comes from the atmosphere. But there is a problem….

The threat of cavitation

Physicists say that liquid water under tension (ie, negative pressure) is in an instable state and may at any time vaporize. This rapid phase transition from liquid to vapor occurs by a process called "cavitation". Cavitation provokes the sudden breakdown of a water column under tension. The rope breaks, and the mechanism of sap ascent is disrupted. Cavitation provokes an air-embolism, i.e. a blockage of the water flow by the presence of air bubbles in the xylem pipes. And of course, leaves are no longer irrigated and dehydrate.

Hopefully, cavitation occurs only when sap tension exceeds a critical value specific to each plant type. This threshold is determined by the porosity of the walls that connect xylem pipes together. Higher porosity favors sap ascent but increases the risk of cavitation. Interestingly enough, species growing in drier habitat (and potentially more drought resistant) tend to be more resistant to cavitation.

The critical xylem tension provoking cavitation is much higher than the tension well watered plants are exposed to on a daily basis. Therefore, cavitation is not routine in plants, and this phenomenon occurs only under exceptional drought conditions. Cavitation reflects a xylem dysfunction.

Understanding drought

Drought lowers the amount of water in the soil. As a consequence of drought, the tension of water in the soil increases (again, a matter of capillary forces). Therefore, tension in the xylem sap must increase to extract water from the soil. The drier the soil, the higher the tension in the xylem pipes. This ‘static’ xylem tension is additive to the ‘dynamic’ tension caused by evaporation.

When the xylem tension approaches the threshold tension provoking cavitation, stomata close which lowers leaf evaporation and hence the ‘dynamic’ sap tension. Stomatal closure maintains the tension below the critical value and hence controls the risk of cavitation. Don’t ask how stomata do that, all we know is that they do it very efficiently! But of course, if you still remember what I said 2 minutes ago, stomata close at the cost of less photosynthesis and less growth. The prevention of xylem hydraulic failure by stomatal closure can expose plant to a potential risk of carbon starvation.

If drought increases further, stomata close completely and, eventually, cavitation occurs. Plant are then in their survival mode. If the degree of cavitation remains low at the end of the drought episode, leaves can recover their function and produce more sugar to make new xylem pipes. Some species can generate positive root pressures to refill embolised pipes, but this is quite rare. If drought has induced more cavitation, plants can still recover but only partially and they may eventually die because plants that are less injured are more competitive. Finally, above a threshold cavitation level, plants never recover and die of hydraulic failure. This critical level of cavitation was found around 50% and 90% for conifer and woody angiosperms, respectively.

This is the most consistent and parsimonious explanation of plant hydraulics. Alternative explanations are occasionally proposed, but it will take you more time to figure them out and, honestly, it is a waste of time trying to understand them!